

PHORID FLIES FOR THE BIOLOGICAL SUPPRESSION OF IMPORTED FIRE ANT IN
TEXAS: REGION SPECIFIC CHALLENGES, RECENT ADVANCES
AND FUTURE PROSPECTS

Lawrence E. Gilbert and Richard J.W. Patrock

Section of Integrative Biology and Brackenridge Field Laboratory
The University of Texas, Austin 78712

ABSTRACT

At the University of Texas' Brackenridge Field Laboratory we maintain one of two laboratories in the U.S. devoted to research on the basic biology of *Pseudacteon* phorid flies, a diverse genus of fire ant parasitoids. Goals include 1) screening various South American species of *Pseudacteon* for their potential to negatively impact the red imported fire ant, *S. invicta*, 2) testing prospect species for their host specificity, 3) developing methods for rearing candidate species, and successfully introducing them to Texas, and 4) monitoring impact of fire ant phorids on local ant community organization.

Challenges in introducing tropical *P. tricuspis* to control *S. invicta* populations across central and south Texas include the 1) high rate of polygyny in *S. invicta* populations and 2) harsh, unpredictable climate of the region. Nevertheless, field-bred *P. tricuspis* have been recovered in 9 of 15 experimental release sites over periods up to 27 months. In South America, we have collaborated with colleagues to study the life histories, geography, and seasonal phenologies of little known *Pseudacteon* species such as *P. cultellatus*. Our laboratory experiments have shown that different species of *Pseudacteon* vary in the extent to which they disrupt the foraging activities of fire ants. Laboratory experiments revealed the negative impact of *P. tricuspis* on colony protein consumption which ultimately affects colony fitness. Our results from various investigations lead to the conclusion that in Texas, biological control of fire ants using phorid flies will likely require more than a single species of *Pseudacteon*, as well as region-specific tactics.

INTRODUCTION

The association of phorid flies of the genus *Pseudacteon* with fire ants has been known since W.M. Wheeler and C.T. Brues studied the biology of *Solenopsis geminata* in central Texas early in the 20th century (Coquillett 1907; Brues 1907). Until the 1990s, research on *Pseudacteon* was primarily taxonomic, but their association with disturbed nests of the genus *Solenopsis* was noted in the descriptions of many species. Efforts in the early 1970's to find biological controls for *Solenopsis invicta* Buren (Hymenoptera: Formicidae) in South America identified *Pseudacteon* among other possible agents (Williams 1973; Williams 1974). While these phorids were subsequently considered possible candidates for biological control of *S. invicta* (Williams et.al. 1973), efforts were not sufficient to assess the details concerning phorid/ant interactions. From the perspective that sought biological agents that imposed high mortality rates on target pest species, *Pseudacteon* species showed little apparent promise and were not pursued by those researchers. The work of Feener

(1981) stimulated interest in *Pseudacteon* phorids as potential biological control agents for fire ants. Studying competition between *Pheidole dentata* Mayr and *Solenopsis texana* Emery at Brackenridge Field Laboratory (BFL) in Austin Texas, Feener demonstrated that the presence of phorids which attack *P. dentata* majors shifted the outcome of competitive interactions with *Stexana*. Without phorids, *Pheidole* always won control of food baits. With phorids *Solenopsis* won. Feener's demonstration of the behavioral effects that phorids impose on ant workers indicated that the primary impacts of these parasitoids on ant colony fitness should be indirect via reducing food intake (especially in the context of competition with other organisms) rather than by the direct mortality of workers.

Feener's hypothesis, extended to imported fire ants, predicted that an important difference between native non-pest *S. geminata* F. and the invasive pest *S. invicta* is that the latter has escaped its *Pseudacteon* fauna. Morrison (2000a; 2000b) has recently shown the way that *Pseudacteon* specific to *S. geminata* (*P. browni* Disney, *P. bifidus* Brown and Morrison, *P. spatulatus* Malloch) reduce that species' ability to compete for food with *S. invicta* in Texas. Does freedom from phorid pressure in its introduced range account for the ability of *S. invicta* to replace *S. geminata* (e.g., Porter et al. 1988)? In Brazil, *Pseudacteon* often alter the ability of *S. invicta* to successfully compete for food resources during the day (Orr et al. 1995; Porter et al. 1995).

These and other observations and experiments underlie the working assumptions of our research program: 1) that *Pseudacteon* phorids ultimately affect the population levels and ecological dominance of host fire ants, and 2) that these parasitoids are a major factor influencing the population and community biology of the North American *Geminata* and South American *Saevissima* species complexes of the genus *Solenopsis*. The latter species complex includes *S. invicta* and more than a dozen related species native to South America.

In fall 2000, USDA APHIS announced an expanded effort to fund the production of *Pseudacteon tricuspis* Borgmeier in partnership with ARS (ARS News Service, November 15, 2000) for release throughout the southern US. This news represented a turning point in terms of official recognition of the potential of biological control of fire ants. More specifically, it identified *Pseudacteon* phorids as one of the leading prospects for reducing the pest status of *Solenopsis richteri* Forel and *S. invicta*. Furthermore the burden of rearing *P. tricuspis*, by that decision, was transferred from the only phorid research laboratory within the USDA, thus allowing it to allocate more attention to fundamental research on less well-known *Pseudacteon* species and their relationships with fire ants.

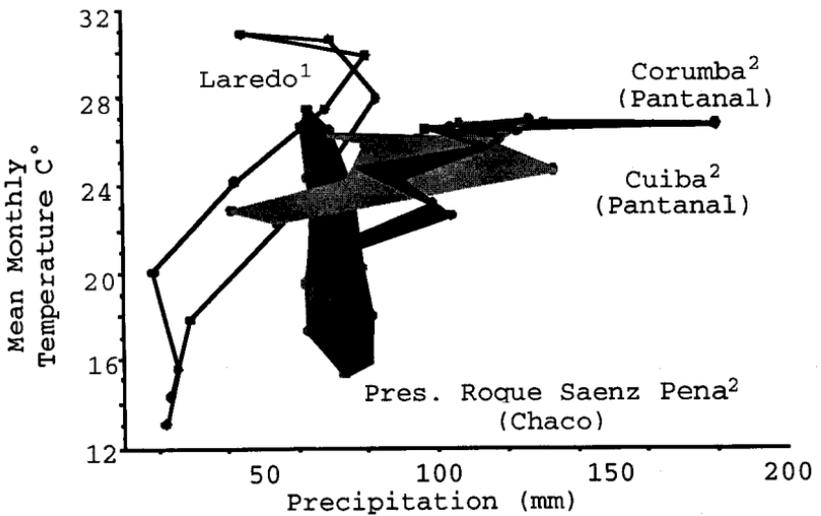
The USDA's commitment to mass-rear and release *P. tricuspis*, the first phorid species (of many possible alternatives) brought into cultivation, should be viewed as a positive initial step. It is difficult to know at this early stage however, if this is the best step possible. It is also unclear whether Brazilian *P. tricuspis* will be effective in Texas. Below, we discuss potential problems of focusing on a single species of phorid fly for biological control of the red imported fire ant over the large geographical range in the United States now occupied by this ant.

REGION SPECIFIC CHALLENGES FOR THE USE OF *Pseudacteon tricuspis*

There are compelling arguments for separate, but cooperating efforts to develop different phorids for fire ant suppression. First, the biogeographic patterns and ecogenotypic diversity within the genus *Pseudacteon* are relatively unexplored subjects. Second, the range now occupied by invading *S. invicta* in the US is highly diverse, both edaphically and climatically. In fact, additional research teams are needed to complement those in Florida and Texas if we are to rapidly explore the full potential of phorid flies across a diverse ecological template, which now includes parts of Arizona and California.

Two region-specific challenges, important when considering the application of phorid flies to suppression of fire ants in Texas, are special foci of our research group. The

first major challenge is the harshness and unpredictability of the Texas climate. Both Gainesville, FL and Austin, TX laboratory cultures of *P. tricuspis* are based on collections originating from several local sites from São Paulo State Brazil, a tropical region with dry and wet seasons. Our initial field release of *P. tricuspis* at BFL in November 1995 was followed by a harsh drought which lasted into August 1996. In 1996, February temperatures began at -9° C and ended at 37° C; extreme monthly records for all Austin weather stations between 1930-2001 (NOAA 2001). Exceedingly arid and warm spring and fall periods have been a frequent feature of Texas climate during the course of our work on phorid releases in Texas (1996-2000). Palmer drought indices place these years as being one of the three driest periods since records have been kept (NOAA 2001). Such dry conditions during the periods when temperatures are generally favorable for tropical phorids make successful establishment of released populations more difficult. Ironically, during these recent droughts, mound densities of fire ant populations also diminished. One consequence of this reduction in fire ant numbers has been the difficulty in obtaining large *S. invicta* colonies with appropriate caste ratios and brood for sustaining/maintaining laboratory cultures of *P. tricuspis*.



¹Data from NOAA (2001)

²Data from Schwerdtfeger (1976)

FIG. 1. Climatograms of relatively harsh areas of Brazil (Pantanal) and Argentina (Chaco) occupied by *Solenopsis* and *Pseudacteon* compared to Laredo, Texas, one of our *Pseudacteon* release sites. Average conditions are both hotter and drier at the Texas site. S. Porter (pers. comm.) suggested these South American sites as possibly comparable to those in Texas.

We are aware of no climatic zones in Argentina or Brazil with *S. invicta* and *Pseudacteon* that can match the extremes of temperature and moisture (see for example, Fig. 1) and lack of predictable dry and wet periods characteristic of central and southern Texas. However, the climatic patterns of some South American regions are more similar to those of Texas than are the source areas for *P. tricuspis* stocks currently being released in

the US. Our working assumption is that phorid species or biotypes from temperate areas will be better able to deal with Texas weather and climate than can tropical *P. tricuspsis* from north of the Tropic of Capricorn. Thus we have initiated preliminary studies in the State of Santiago del Estero, Argentina, the climatograms (Patrock and Gilbert unpub. data) and remarkably convergent vegetation (Gilbert unpub. obs.) of which are similar to those of south Texas.

A second challenge, faced more in the Texas region than elsewhere in the southern US, is the predominance of the polygynous form of *S. invicta* (Porter et al. 1991 and 1992). While high colony densities of polygyne populations should favor the spread of a parasitoid, the peculiar mode of sex determination in *P. tricuspsis* and other large *Pseudacteon* species actually acts to reduce the probability of colony establishment. In these phorids host ant size determines the sex of the phorid larva developing within it (Morrison et al. 1999a). Since the worker size classes that favor female *tricuspsis* are relatively less abundant in polygyne, than in monogyne *S. invicta*, male biased sex ratio is a problem both for maintaining laboratory cultures on locally collected fire ants and for successfully introducing *P. tricuspsis* into *S. invicta* populations in the field. Analysis of *S. invicta* colonies in central Texas indicates that only 4.2% of workers in an average colony are large enough to produce female *P. tricuspsis* exclusively and only 8.3% will produce at least some females (Patrock et al. unpub. data). In contrast, ca. 27% of average monogyne colonies may produce at least some females (data from Greenberg et al. 1985).

Disturbed mounds and mating flights, to which *P. tricuspsis* typically orients for mating and host-finding, are relatively rare in hot, dry weather. Under such conditions, worker fire ants moving along foraging trails may provide the only chance for *P. tricuspsis* to encounter hosts over much of central and south Texas where we have focused our release efforts. Prospects of finding workers large enough to produce female *P. tricuspsis* in this context (on trails) are even more remote than in the case of disturbed mounds. Typical foraging trails possess only a few dozen workers and are typically nocturnal during hot months. Assuming that these groups are random samples of the castes present in local colonies, likelihood of a female *P. tricuspsis* finding a foraging worker fire ant which will support a female phorid offspring during her short (two to four day) life is very small (Patrock et al. unpub. data). Indeed, after a dry and very hot summer and early fall of 2000, followed by continuous cold, wet conditions from mid November 2000 to late March 2001, 80% of *P. tricuspsis* spring generation adults recovered from the naturalized population at BFL in Austin, Texas were male, as predicted by Morrison et al. (1999a). Needless to say, such sex ratios do not allow rapid population expansion by this species under conditions experienced in the release areas to date.

The culture of *P. tricuspsis* established by S.D. Porter from collections in São Paulo State, Brazil, and now mass-reared by USDA ARS (in Gainesville, FL), has been maintained on monogyne *S. invicta* and successful establishment has been documented in monogyne and polygyne populations of *S. invicta*. In the Gainesville area, breeding populations of *P. tricuspsis* have spread from initial release sites to range over at least 3100 sq. km (S. Porter pers. comm.). Early attempts to introduce populations into Texas using both pupae from Porter's cultures and his original pupal release protocol, failed (J. Cook pers. comm. and pers. obs.). However, it is not possible to ascertain the causes for these failed attempts because both drought and polygyny of host ants are potential factors. We have subsequently established *P. tricuspsis* populations in several sites in Texas based on releases of adult flies from a genetically diverse *P. tricuspsis* stock descended from our 1996-98 collections at several sites near Campinas, S.P. Brazil, as well as significant input from the 1998 laboratory culture established by S.D. Porter in Gainesville. These developments are discussed below.

RECENT ADVANCES

A major thrust of our laboratory has been study of the basic biology of *Pseudacteon* phorid flies, including improvement of efficient laboratory production of phorid flies for research on fire ant biological control. Significant accomplishments of these efforts include:

1. Management and improvement of phorid fly mass rearing procedures and experimental facilities in order to increase the production of *P. tricuspsis* and to bring other phorid species (described below) into cultivation.

2. Exploration for new candidate phorid species in South America, study of their phenology and distribution, evaluation of their relative impacts on hosts, and coordinated specificity testing. This work is carried out with cooperators in Brazil and Argentina.

3. Investigations of life history or life cycle constraints (such as harshness of climate or polygyne traits of imported fire ants) to introducing South American phorids in Texas.

With respect to laboratory production of *P. tricuspsis*, we are attempting to balance the production of *P. tricuspsis* for release trials in Texas while maintaining the flexibility to continue experimental work with that and other species of *Pseudacteon*. By maintaining a system of numerous separate attack trays into which ants and flies are introduced daily, we retain both the flexibility to conduct replicated experiments and the ability to maintain selected lines of *P. tricuspsis*. Thus, we continue long term efforts to select for the production of female flies on smaller hosts, and can pursue other selection regimes that might tailor our stocks for Texas conditions (e.g., high temperatures).

We have established protocols for sizes and quantities of host, and numbers and sex ratios of *P. tricuspsis*, which maximize production and minimize effort within the constraints of our research focus (rather than emphasizing mass production of a single stock). During typical periods when adequate ant supplies are available our laboratory has the capacity to produce 1,000 adult *P. tricuspsis* per day using six attack chambers. Of these flies, 250 are reserved for lab culture and the balance can be used in laboratory or field experiments or in field releases. Brazilian *P. tricuspsis* may not prove to be the ideal *Pseudacteon* for central and south Texas. However, it may do well in more mesic eastern Texas (see below) and it continues to be an important tool for better understanding the life history of ant-attacking phorids and their impact on host ants. Our approach to rearing it will be compatible with shifts to mass culturing other species as that becomes feasible and desirable.

With respect to other species of *Pseudacteon*, we have demonstrated in the laboratory that species may vary both in details of oviposition behavior and in how intensely fire ant workers respond to their oviposition attacks (Wuellner et al. 2002). We have also maintained several additional *Pseudacteon* species through multiple generations. These include the Argentinean species, *P. cultellatus* Borgmeier (Folgarait et al. 2002), as well as Brazilian forms of *P. curvatus* Borgmeier and *P. litoralis* Borgmeier. The latter species produces females from workers larger than those suitable for *P. tricuspsis* (Morrison et al. 1999a). While *P. litoralis* may not be suited for our focal study areas, it may do well in much of the southeastern US including eastern Texas, or elsewhere where monogyne colonies predominate. Our policy will be to transfer such stocks, once well established, to other laboratories for trials in Florida and the southeastern US.

In seeking new species or ecotypes of *Pseudacteon* for study, we are particularly interested in small species that 1) attack workers along foraging trails, 2) attract smaller, more abundant size classes of workers, and 3) fall below the size preference threshold of *P. tricuspsis* (for reasons explained above). One small species, *P. curvatus*, from Argentinean *S. richteri* stocks, has been cultured on *S. invicta* and released by S.D. Porter and collaborators. Although his *P. curvatus* stock has established on US populations of *S. richteri* and *S. richteri* x *S. invicta* hybrids, it apparently has not yet been established on *S. invicta*

populations into which it has been introduced several times (Porter 2000; Porter pers. com. 2000).

We prefer to proceed conservatively in the case of *P. curvatus*. The Brazilian stocks (collected from *S. invicta*) which we tested for host specificity did not discriminate between *S. invicta* and *S. geminata* (Gilbert and Morrison 1997). Even if *P. curvatus* do not do well at parasitizing *S. geminata* (Porter 2000), they might speed the demise of this native fire ant as they “spill over” from vastly more abundant *S. invicta*. We know *Pseudacteon*-free *S. invicta* possesses an exploitative advantage over *S. geminata* in Texas contact zones where the latter is attacked by a suite of native *Pseudacteon* (Morrison 2000a). From our knowledge of the system, *S. invicta* specialist phorids are more likely to return parity between these competing congeners. Moreover, presence of an abundant non-specialist phorid generated by *S. invicta* will impose an indirect effect on *S. geminata* in its competition with other ant genera.

Our concern about *P. curvatus* in Texas extends to the fate of *S. geminata*-specialist phorids, which are an unexploited source of information on how native *Pseudacteon* survive in Texas. These native phorid species are disappearing as their host ant disappears. Of course, such a process continues anyway as *S. invicta* populations exclude local populations of *S. geminata* (e.g., Porter et al. 1988). However, given such uncertainty about the potential impact of *P. curvatus* and the availability of other small phorids, such as *P. obtusus* Borgmeier (Morrison and Gilbert 1999), we view the use of *P. curvatus* in Texas as a last resort measure. However, in other regions where this native fire ant-phorid system does not exist, *P. curvatus* may be viewed as a reasonable consideration given the cost of letting fire ants continue to dominate and spread (Porter 2000).

Pseudacteon curvatus, like *P. tricuspsis*, is typically encountered at mound disturbance events (Orr et al. 1997). Consequently, it is easy to collect large numbers by focusing efforts around several artificially disturbed mounds. By contrast, several other small *Pseudacteon* patrol small trails of workers from the exit of an underground tunnel to the piece of food being harvested. The specialists among this category of *Pseudacteon* are the main priority of our current and future efforts to develop new species cultures for testing. However, they impose two problems: 1. They tend to be more diffusely distributed thus making them harder to find and collect and 2. Adults are very small and do not survive transit from South America to Texas as well as do those of larger species.

To overcome these logistic difficulties, we established collaboration in Argentina with Dr. P.J. Folgarait (Universidad Nacional de Quilmes, B.A, Argentina). Her laboratory is the first facility in South America designed to culture and study *Pseudacteon*. By raising these less common species (e.g., *P. cultellatus*) in her laboratory in Buenos Aires, it has been possible to obtain a critical mass of pupae for shipping to the BFL rearing facility. With her laboratory as a base, we have been able to study the phenology (Folgarait et al. unpub. data) and life histories (Folgarait et al. unpub. data) of numerous little known *Pseudacteon* species. This work, plus a study (in progress) of the biogeography of South American *Pseudacteon* (Folgarait et al. unpub. data.) is helping identify regions where useful species and ecotypes might be sought.

The emphasis on exploring for phorid species in seasonal and/or more drought-prone regions of Argentina has been driven to some extent by our experience with the fate of released *P. tricuspsis* in Texas (see below) and on the results of experiments to explore the biology of diapause in this Brazilian stock of *P. tricuspsis*. To date, and following substantial experimental effort, we have no compelling evidence that this tropical *P. tricuspsis* enters diapause (Wuellner pers. comm.). On the other hand, phenological patterns within a single community of Argentine *Pseudacteon* (Folgarait et al. unpub. data) strongly suggest diapause strategies, which might allow some species to deal with some of the most extreme climates of *S. invicta*-invaded regions.

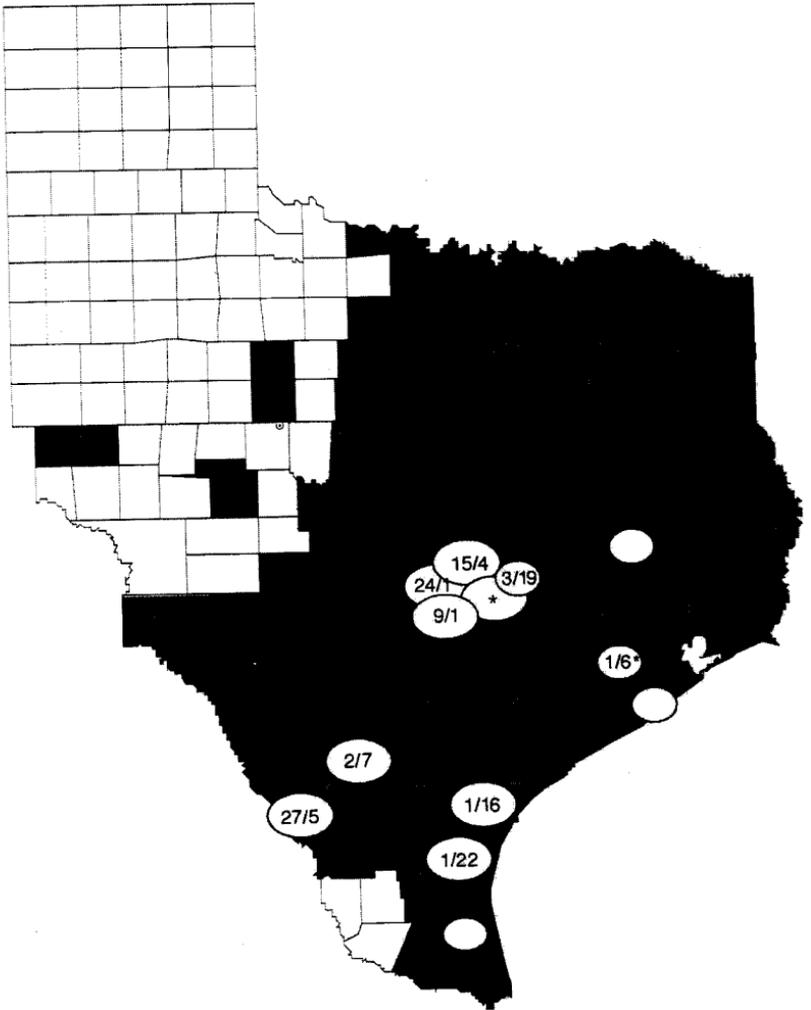


FIG. 2. Map of *Pseudacteon tricuspis* release sites in Texas (1998-2001). Gray region shows counties under fire ant quarantine. Oval centered over release area indicates time, in months, that monitoring efforts demonstrated presence of naturalized *P. tricuspis* in the numerator and months since last fly detected at each site (as of November 2001) in the denominator. Blank ovals indicate areas where phorids have not established (as of November 2001). Asterisks indicate areas with releases too recent to obtain results. Two unsuccessful sites near Laredo are not shown.

EXPERIMENTAL FIELD RELEASES

Another major thrust of our project utilizes South American phorids as biological controls of fire ants. This work has included monitored field introductions of *Pseudacteon tricuspis* at 15 sites in central and south Texas at which preliminary surveys revealed a substantial presence of native ants (see Fig. 2). Because the anticipated impact of phorid pressure on *S. invicta* is a shift in its competitive status with respect to native ants, baseline studies of distributions and interactions of native ants and *S. invicta* are conducted at each site to allow refined assessments of the effectiveness of phorids in shifting the balance of power towards the native ant community.

On the positive side, naturalized adult phorids detected during periodic monitoring demonstrate the establishment of *P. tricuspis* on Texas fire ant populations at 9 of the 15 release sites (see Fig. 2). Since *P. tricuspis* males and females orient to disturbed mounds (Orr et al. 1997), observations at disturbed mounds is a standard method for detecting this species. However, because severe drought reduced the number of active mounds at many of our sites since 1998, we monitor for phorid presence using white plastic trays containing midden material (primarily dead fire ant bodies) from laboratory colonies to attract both sexes of *P. tricuspis*. They visit such midden trays in areas with no visible mounds nearby, well away from points of release (i.e., greater than 100 meters).

To date, however, none of the *P. tricuspis* populations initiated in central and south Texas have attained the apparent density of native phorids that attack native ants such as *Pheidole* or *S. geminata* (Patrock and Gilbert pers. obs.) nor have they achieved densities or rates of spread reported from Florida releases (Porter pers. com.). Although not the desired result, this is an important finding which should direct most future efforts with *P. tricuspis* in Texas to the more mesic, eastern parts of the state. Unfortunately, because the dual constraints of drought and polygyny are confounded at all of our current release sites, we are unable to determine which, if either, is the more important factor for this phorid species. If our study region eventually enters an extended period of mild, moist conditions and our introduced populations expand as they have in Florida, then we must consider the possibility that polygyny is a less important constraint for *P. tricuspis* than we now think it is.

STRAIN SELECTION EFFORTS

These initial results with *P. tricuspis* in Texas were anticipated based on our studies of the relationship between host size and fly sex determination/sex ratio (Morrison and Gilbert 1998; Morrison et al. 1999). We therefore selected for and reared a stock of *P. tricuspis* based on small females that eclose from workers size classes that typically produce males, the goal being to develop a selected line that will produce more favorable sex ratios on polygyne *S. invicta*.

While such selection is likely to occur naturally in the field, post-selection female densities may be below critical threshold for establishing a population. Increasing optimum genotypes under laboratory protection is one way to insure that possible and desirable evolutionary changes actually happen. We were able to alter sex ratios of our "small *P. tricuspis*" line reared on small majors from strongly male biased to near unity over a few generations (unpub. data). An important issue, yet to be determined, is whether this "small *P. tricuspis*" line has been more successful in its establishment than the source stock (both have been released at all sites). Currently, we are applying Amplified Fragment Length Polymorphism (AFLP) analysis to genetically characterize laboratory cultures, as well as phorids recovered in the field, with the goal of understanding the value of selectively modifying laboratory lines to produce females on smaller host workers.

Modification of existing stocks by selection or genetic engineering may be a more time-consuming and costly approach than tapping the existing genetic library of *Pseudacteon* biodiversity in South America. For example, there is strong indication that some *Solenopsis*-attacking *Pseudacteon* employ mechanisms other than host size for determining sex (Folgarait and Gilbert unpub. obs.). Such species may have the plasticity to better deal with polygyne fire ants in Texas. Moreover, since phorids undoubtedly exist on the few polygynous populations of *S. invicta* in its native range, those populations are a potential source of *P. tricuspis* ecotypes already tailored to our needs.

ENVIRONMENTAL CONSTRAINTS

With respect to the problem of climate, it is progress to be aware that we do not yet understand just how abiotic conditions constrain establishment and spread of *P. tricuspis*. At BFL in fall 2000, we observed flies arriving at our artificial middens in ambient temperatures above 40° C and during a period of extended drought. Thus, adult phorids are able to seek hosts under such conditions. However, because there were very few host fire ants active above ground, it seems unlikely that these short-lived (two to three days) adult flies have great reproductive success under such circumstances. Investigators who rear these organisms have also learned that immature *P. tricuspis* do not survive temperature extremes in laboratory conditions either.

Additional correlates of harsh drought conditions include reduction of fire ant mound densities, shifts in colony caste ratios under stress of drought, and increasing patchiness of active mound distributions as *S. invicta* colonies concentrate around moist areas. *Pseudacteon* egg to adult period is 30-40 days and adult life span is 2-3 days. Thus the extended (> 1.5 months) dry, hot conditions frequently experienced in our region since 1996 would indeed seem to pose a major problem for establishment and spread of *P. tricuspis*.

As with the constraint of polygyny, that of climate is probably best circumvented by tapping the existing biodiversity within and between *Pseudacteon* species that are already adapted to Texas-like arid climates in South America. Seeking pre-adapted ecotypes and species may ultimately be a strategy more likely to succeed than waiting for introduced *Pseudacteon* to evolve all the right traits for a particular region.

LABORATORY EXPERIMENTS

Our past release efforts have helped us think more clearly and realistically about what constraints must be overcome to establish phorids in Texas at densities needed to impact the fitness of imported fire ant colonies. But controlled experiments are required to understand the potential of phorids to affect colonies. Our laboratory studies of colony-level impacts of phorids on *S. invicta* (Mehdiabadi and Gilbert unpub. data) show that one attacking phorid per approximately 200 foraging workers can reduce colony protein intake by 50%. These and related results provide parameter values for development of predictive models on the rates of change that can be expected at various levels of 'phorid pressure' in the field.

FUTURE PROSPECTS

Our field and laboratory investigations of the phorid/fire ant interaction maintain our optimism that *Pseudacteon* phorid flies will become part of the eventual biological solution to the problem of imported fire ants. But just as these insects will be only part of the solution over part of the introduced range of imported fire ants, so too is it likely that *P. tricuspis* will be but a part of the phorid component of any eventual biological solution to this problem.

Indeed, we have suggested why, in regions like Texas, other *Pseudacteon* species or suites of species are more likely to establish at the levels needed to exert influence on the competitive status of imported fire ants in the local ant community.

No social insect pest has ever been successfully controlled with biological enemies. Therefore, solving the fire ant problem is a challenging exercise in applied evolutionary and community ecology. In our view, phorid research to date has only exposed the tip of an iceberg of possibilities with respect to applying the genus *Pseudacteon* to fire ant biocontrol. The apparent biotic and abiotic barriers to introducing *Pseudacteon tricuspis* in Texas, as outlined above, have determined the agenda for our current and future research program.

ACKNOWLEDGMENT

We acknowledge the substantial support of The State of Texas Fire Ant Research and Management Project (FAARMAC). Additional support from The Robert J. Kleberg and Helen C. Kleberg Foundation, The Fondren Foundation, and the Houston Livestock Show and Rodeo have provided important flexibility and the ability to support South American collaborators. USDA APHIS and U.S. Fish and Wildlife Service provided permits for importation of *Pseudacteon*. Permits to colleagues W.W. Benson in Brazil from CNPq and IBAMA, and to P.J. Folgarait from Direccion de Fauna and Flora in Argentina, allowed exportation of phorids from those countries for studies in Texas. We acknowledge intellectual input from P. Folgarait, C. Wuellner, N. Mehdiabadi, S. Porter, and L. Morrison. We are grateful to the technicians and staff at Brackenridge Field Laboratory for their crucial efforts to collect fire ants, rear phorids, and help with fieldwork. We thank Mr. Ben Vaughan for important logistic support. We acknowledge The University of Texas at Austin for its support of the BFL facility. We appreciate the efforts of all those who reviewed the first version of the manuscript.

LITERATURE CITED

- Brues, C.T. 1907. On the phorid genera *Plastophora* and *Pseudacteon*. Entomol. News. 18: 430.
- Coquillett, D.W. 1907. A new phorid genus with horny ovipositor. Can. Entomol. 39: 207-208.
- Feener, D.H., Jr. 1981. Competition between species: outcome controlled by parasitic flies. Science 214: 815-817.
- Folgarait, P.J., O.A. Bruzzone, and L.E. Gilbert. 2002. Development of *Pseudacteon cultellatus* (Diptera: Phoridae) on *Solenopsis invicta* and *Solenopsis richteri* fire ants. Environmental Entomology (In Press).
- Gilbert, L.E. and L.W. Morrison. 1997. Patterns of host specificity in *Pseudacteon* parasitoid flies (Diptera: Phoridae) that attack *Solenopsis* fire ants (Hymenoptera: Formicidae). Environ. Entomol. 26: 1149-1154.
- Greenberg, L., D.J.C. Fletcher, and S.B. Vinson. 1985. Differences in worker size and mound distribution in monogynous and polygynous colonies of the fire ant, *Solenopsis invicta* Buren. J. Kansas Entomol. Soc. 58: 9-18.
- Morrison, L.W. 2000a. Mechanisms of *Pseudacteon* parasitoid (Diptera: Phoridae) effects on exploitative and interference competition in host *Solenopsis* ants (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. 93: 841-849.
- Morrison, L.W. 2000b. Mechanisms of interspecific competition among an invasive and two native fire ants. Oikos. 90: 238-252.
- Morrison, L.W. and L.E. Gilbert. 1998. Parasitoid-host relationships when host size varies: the case of *Pseudacteon* flies and *Solenopsis* fire ants. Ecol. Entomol. 23: 409-416.

- Morrison, L.W. and L.E. Gilbert. 1999. Host specificity in two additional *Pseudacteon* spp. (Diptera: Phoridae), parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae). *Florida Entomol.* 82: 404-409.
- Morrison, L.W., E.A. Kawazoe, R.D. Guerra, and L.E. Gilbert. 1999b. Phenology and dispersal in *Pseudacteon* flies (Diptera: Phoridae), parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* 92: 198-207.
- Morrison, L.W., E.A. Kawazoe, R. Guerra, L.E. Gilbert. 2000. Ecological interactions of *Pseudacteon* parasitoids and *Solenopsis* ant hosts: environmental correlates of activity and effects on interspecific competition. *Ecol. Entomol.* 25: 433-444.
- Morrison, L.W., S.D. Porter, and L.E. Gilbert. 1999a. Sex ratio variation as a function of host size in *Pseudacteon* flies (Diptera: Phoridae), parasitoids of *Solenopsis* fire ants (Hymenoptera: Formicidae). *Biol. J. Linn. Soc.* 66: 257-267.
- NOAA. 2001. <http://www.ncdc.noaa.gov/ol/climate/stationlocator.html>
- Orr, M.R., S.H. Seike, W.W. Benson, and L.E. Gilbert. 1995. Flies suppress fire ants. *Nature* 373: 292-293.
- Orr, M.R., S.H. Seike, and L.E. Gilbert. 1997. Foraging ecology and patterns of diversification in dipteran parasitoids of fire ants in south Brazil. *Ecol. Entomol.* 22: 305-314.
- Porter, S.D. 2000. Host specificity and risk assessment of releasing the decapitating fly *Pseudacteon curvatus* as a classical biocontrol agent for imported fire ants. *Biol. Control* 19: 35-47.
- Porter, S.D., A.P. Bhatkar, R. Mulder, S.B. Vinson, and D.J. Claire. 1991. Distribution and density of polygyne fire ants (Hymenoptera: Formicidae) in Texas. *J. Econ. Entomol.* 84: 866-874.
- Porter, S.D., H.G. Fowler, and W.P. Mackay. 1992. Fire ant mound densities in the United States and Brazil (Hymenoptera: Formicidae). *J. Econ. Entomol.* 85: 1154-1161.
- Porter, S.D., R.K. Vander Meer, M.A. Pesquero, S. Campiolo, and H.G. Fowler. 1995. *Solenopsis* (Hymenoptera: Formicidae) fire ant reactions to attacks of *Pseudacteon* flies (Diptera: Phoridae). *Ann. Entomol. Soc. Am.* 88: 570-575.
- Porter, S.D., B. Van Eimeren, and L.E. Gilbert. 1988. Invasion of red imported fire ants (Hymenoptera: Formicidae): microgeography of competitive replacement. *Ann. Entomol. Soc. Am.* 81: 913-918.
- Schwerdtfeger, W. 1976. *Climates of Central and South America. World Survey of Climatology. Vol. 12.* Elsevier Scientific Pub., NY.
- Williams, R.N., J.R. Panaia, D. Gallo, and W.H. Whitcomb. 1973. Fire ants attacked by phorid flies. *Fla. Entomol.* 56: 259-262.
- Williams, R.N. and W.H. Whitcomb. 1974. Parasites of fire ants in South America. *Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage.* 5: 49-59.
- Wuellner, C., C. G. Holvorcem, W.W. Benson, and L.E. Gilbert. 2002. Phorid fly (*Pseudacteon* spp.) oviposition behavior and attacked red imported fire ant response differ according to fly species. *Ann. Entomol. Soc. Amer.* 95: 257-266.